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Diagnostic characteristics of subfamilies of the Tubificidae family (Oligochaeta)

by N.P. Finogenova

The following important characteristics have been singled out and a key to the subfamilies of the Tubificidae has been compiled on the basis of them: the presence or absence of large coelomocytes in the body cavity, the mode of attachment, form and number of prostatic glands on each male gonoduct, the location of the spermathecal pores, the nature of the male sexual cells. A new subfamily, Nootkadrilinae, has been established for two marine genera. The composition (at the genus level) is given for all seven subfamilies. The description of Svetlovia maculata Cekanovskaja has been expanded following a review of the holotype of this species.

There have been many attempts to establish order in the family Tubificidae, the members of which are widely distributed in fresh and marine waters. Initially, two subfamilies, Tubificinae and Telmatodrilinae, were distinguished among the tubificids (Eisen, 1879). Somewhat later (Stolc, 1885, 1888), another two subfamilies, Ilyodrilinae Stolc, 1885 and Bothrioneurinae Stolc, 1888, were established. Ilyodrilinae was recently renamed Rhyacodrilinae by Hrabe (1963) on the basis that Ilyodrilus coccineus Vejd., now a synonym of Rhyacodrilus coccineus (Vejd.), served as its type species. Many new forms of tubificids have been described over the past two decades as a result of more intensive research.

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Interpretation of the constantly accumulating morphological material resulted in revisions of old concepts, diagnoses and criteria. Our concepts of the subfamilies of tubificids also changed.

Hrabe (1966) proposed that the genus Branchiura Bedd., with its distinctive structure of the genital organs and a number of unusual somatic characters, be established as a separate subfamily, Branchiurinae, and later (Hrabe, 1967) that Aulodrilus Bretsch. be established as the subfamily Aulodrilinae. Chekanovskaya accepted the subfamilies established by Hrabe, but did not agree with the establishment of the subfamily Telmatodrilinae, regarding its genera Telmatodrilus Eisen and Alezandrovia Hrabe as part of the Tubificinae. Brinkhurst (1971) established another subfamily, Phallodrilinae, for the group of marine forms, and removed the previously known marine genus Clitellio Sav. from the Tubificinae and established it as an independent subfamily, Clitellinae. By the way, this genus was again returned to the subfamily Tubificinae in 1979 (Brinkhurst, Baker, 1979). Furthermore, the same author (Brinkhurst, 1971) placed Bothrioneurum Stolc in the subfamily Rhyacodrilinae, thus abolishing the monotypic subfamily Bothrioneurinae, and later (Brinkhurst, 1981) assigned the genus Branchiura Bedd. to the same subfamily, eliminating the second monotypic subfamily Branchiurinae. Finally, Erseus (1982) established the new subfamily Limnodriloidinae on the basis of several marine genera.

The size of the subfamilies did not remain fixed. The composition of many of the subfamilies (especially the marine ones) was expanded with redescribed forms, and altered as a result of the

(195)

shifting and revision of already known genera. Various characters, but mainly the structural characteristics of the generative organs were used as criteria for substantiating the subfamilies. For example, in his brief diagnosis of the subfamilies Telmatodrilinae and Tubificinae, Eisen (1885) indicates several prostatic glands on the atrium and a distinctive penial structure for the first subfamily, and one prostatic gland on the atrium and a different penial structure for the second subfamily, noting these as the most characteristic features of these subfamilies. To differentiate Ilyodrilinae (now Rhyacodrilinae) and Tubificinae, Stolc (1885) also includes such characteristics as the form of the prostatic gland, the presence or absence of spermatophores, Naidomorpha (Rhyacodrilinae)-type or Tubificinae-type development of the eggs , the presence or absence of genital setae, as well as the form of the penial apparatus.

Hrabe (1963, 1966, 1967, 1979), who has made a great contribution to the basic concepts of oligochaete morphology and systematics, also proceeds from the features characterizing the genital organs, and in addition uses several somatic characters. He believes that the following characters are the most important for the differentiation of tubificids into subfamilies: 1) the form (diffuse or separate) and number (one or several) of prostatic glands; 2) the form of the male sexual cells (spermatozoa or spermatozeugmata); 3) the location of the spermathecal pores (at the anterior dissepiment or in the middle of the segment); 4) egg formation (maturation of the eggs in partial ovaries or singly); 5) the presence or absence of a true penis; 6) the form of the nephridia (with a

sacciform postseptale of the enchytraeid type or in the form of unfused loops); 7) the presence or absence of large coelomocytes in the body cavity; 8) the presence or absence of dorsal pores, and in addition to this a number of characters typical of the genera Bothrioneurum and Branchiura when distinguishing the subfamilies Bothrioneurinae and Branchiurinae.

Brinkhurst (1971) believes that the only important and convenient characters are Nos. 1, 2 and 7 which, in his opinion, have the advantage that they are almost always mentioned in the descriptions of tubificids, and so the family is easily classified into groups on the basis of these characters. However, as we have already mentioned, the author himself was not quite satisfied with the tubificid system and continued to improve it by means of rearrangements. By the way, in his 1981 paper (Brinkhurst, 1981), he used yet another Hrabe character in the diagnosis of Rhyacodrilinae, namely the location of the spermathecal pores.

If we take the genera Branchiura and Bathrioneurum as part of the Rhyacodrilinae (which we believe to be correct), then the 4th, 6th, 7th and 8th characters in their description (partial ovaries sacciform postseptale of nephridia, large coelomocytes and dorsal pores present) are typical only of this subfamily, and not necessarily for the whole series of forms. For example, there are no partial ovaries in Bothrioneurum, Rhizodrilus and Paranadrilus, and for some genera the nature of oocyte formation is unknown; there are no sacciform postseptale of the nephridia in Rhyacodriloides, Rhizodrilus and Branchiura, and for some genera there are no data on this; dorsal pores are noted only in Epirodrilus, Rhyacodrilus and Bothrioneurum, while the rest of the genera either

have none or nothing is known about them; coelomocytes are known for 18 genera, are sometimes missing in one genus, and are never found in three genera. Thus, the listed characteristics merely emphasize the distinctiveness of the Rhyacodrilinae.

As to the form of the penis (5th characteristic), it may be found, within the same subfamily, in the form of a pseudopenis or a true penis (in several subfamilies). Among the Phallodrilinae, for example, 6 genera have simple pores, 4 genera pseudopenises, and 5 genera penises (2 of the latter with chitinous cover as in the Tubificinae); among the Telmatodrilinae, one genus has a penis, and one genus a pseudopenis; among the Rhyacodrilinae, 3 genera have a penis, 8 genera pores, and 10 genera a pseudopenis. (196)

A study of the vast and diverse morphological material on tubificids published recently has confirmed the importance of the following characters to the classification of this family into subfamilies: 1) the presence (as the most universal character for Rhyacodrilinae) or absence of large coelomocytes in the body cavity; 2) the mode of attachment, the form and the number of prostatic glands on each male gonoduct; 3) the location of the spermathecal pores; 4) the nature of the male sexual cells. On the basis of these characters, the following determination table has been drawn up for the subfamilies of the Tubificidae.

1 (2) Large (sometimes comparatively small, but numerous) coelomocytes usually present in body cavity (if not, then prostatic gland diffuse)..... Rhyacodrilinae

2 (1) No large coelomocytes.

3 (8) Spermathecal apertures near anterior (as an exception, posterior) dissepiment (in individual rare cases, in middle of segment).

4 (5) Each male gonoduct with more than two prostatic glands..... Telmatodrilinae

5 (4) Each male gonoduct with not more than two prostatic glands.

6 (7) If present, prostatic glands compact, often stalked, less commonly with wide base..... Phallodrilinae

7 (6) One prostatic gland stalked, second one diffuse or absent..... Nootkadrilinae subfam. n.

8 (3) Spermathecal apertures approximately in middle of segment (rarely offset anteriorly or posteriorly)

9(10) One prostatic gland broadly attached to prostatic pad of atrium or its diverticulum..... Limnodriloidinae

10(9) One prostatic gland attached to atrium by means of a stalk.

11(12) Spermatozoa present..... Aulodrilinae

12(11) Spermatozeugmata present..... Tubificinae

Along with the characters indicated in the table, we shall note a number of other important features, as well as the size of the subfamily.

RHYACODRILINAE HRABE, 1963

The somatic setae differ; they may be forked, single-toothed, three-toothed, sometimes with a ligament connecting the lower tooth to the shaft of the seta, fan-shaped or hairlike. Genital setae are often present. Dorsal setae are sometimes present. The nephridia often have a sacciform postseptale. The male gonoducts have a diffuse (individual cells or groups of cells) prostatic gland. Copulatory glands are sometimes present; they are often histologically similar to the prostatic tissue (e.g. in Macquaridrilus). Sometimes there are no prostatic cells. The male genital apparatus consists of simple pores or pseudopenises (sometimes in coelomic sacs); true penises are rare. The spermathecae are paired, rarely

unpaired; they open in segment X near the anterior (very rarely posterior) dissepiment, sometimes in the posterior part of segment IX, and sometimes they are absent. Heterodriloides has 2 pairs of spermathecae in segments XI and XII. The spermatozo constitute a free mass; they are very rarely found in organized clusters. Morulae of oocytes form during oogenesis in some genera.

This subfamily includes the following genera: Epirodrilus Hr., Rhyacodrilus Bret., Svetlovia Cekanovskaja, Paranadrilus Gavrilov, Protuberodrilus Giani et Martinez-Ansemil, Branchiura Beddard, Bothrioneurum Stolc, Peristodrilus Brinkhurst, Rhizodrilus Smith, Monopylephorus Lev., Rhyacodriloides Cakanovskaja, Jolydrilus Marcus, Ainudrilus Finogenova (=Vadicola Baker), Lymphachaeta Snimschikova, Heterodrilus Pierant., Heterodriloides Erseus, Gieredrilus Erseus, Macquaridrilus Jamieson and Heronidrilus Erseus et Jam. (197

Coelomocytes (the most characteristic feature of this subfamily, which is not noted in any of the other subfamilies) are not found in Rhyacodriloides, Branchiura or Lymphachaeta, and are not always noted in Rhizodrilus pacificus. It may be that they are confined to certain stages of the life cycle, and so they may be absent during certain periods.

The genus Svetlovia was established by Chekanovskaya (1975) for the abyssal Baikal species S. maculata. Our study of the holotype resulted in a change and expansion of its initial description.

Svetlovia maculata Cekanovskaja

Holotype. There are two pairs of testes in segment IX, as noted by Chekanovskaya, and another pair of smaller ones in segment

VIII. The spiral vas deferens measuring about 250 µm in length falls apically from the side into the atrium which consists of an oval ampulla, a narrow ejaculatory duct and a massive pseudopenis, and not penis as indicated in the initial description (Fig, A). The atrial ampulla has a glandular epithelium (with the exception of the ectal end) and cilia, measures about 200 µm in length and at most 115 µm in width, and has a muscular lining up to 7.5 µm thick. The muscular ejaculatory duct is about 40 µm long and 17.5-30 µm wide, and has a very narrow lumen (2.5-5 µm). The pseudopenis measures 137.5 µm in length, and is 75 µm wide in its central part. Numerous muscle fibres attach the pseudopenis (they are partially present on the ejaculatory duct as well) to the body wall. The penial setae are found behind the pseudopenises. This genus is morphologically similar to Epirodrilus, but is distinguished from it by the differentiation of the atrial tube into an ampulla, an ejaculatory duct and pseudopenis, as well as by the presence of cilia inside the atrial ampulla and the uniform thickness of the wall of the parts of the atrial tube.

PHALLODRILINAE BRINKHURST, 1971

The somatic setae are solely forked, sometimes with a ligament connecting the lower tooth with the shaft of the seta; in exceptional cases, there is sometimes a third tooth. Genital setae are often present. Some species have no intestine. The gonoduct in the majority of genera has 2, less commonly one prostatic gland (sometimes absent). In some genera, the ectal prostate (pseudoprostate?) is attached to the base of the penis and (or) to the walls of the penial bursae. The spermatozoa constitute a free

mass, and in exceptional cases round spermatozeugmata.

This subfamily includes the genera Phallodrilus Pierant., Bathydrilus Cook, Aktedrilus Kn., Adelodrilus Cook, Coralliodrilus Erseus, Bacescuella Hr., Inanidrilus Erseus, Olavius Erseus, Jamiesoniella Erseus, Spiridion Kn., Atlantidrilus Erseus, Uniporodrilus Erseus, Bermudrilus Erseus, Peosidrilus Baker et Erseus and Duridrilus Erseus.

Despite the exceptional peculiarity of some of the features of certain genera (unpaired atrium, spermathecae in segment XII, the absence of an intestine, a wide vas deferens without cilia, etc.), this is a highly compact homogeneous group in which we can easily trace the relations between the genera. Erseus (1979) regards the form similar to Phallodrilus as the prototype of many of the genera.

NOOTKADRILINAE FINOGENOVA, SUBFAM. N.

The somatic setae are forked or single-toothed. Penial setae are present. The male gonoducts consist of 4 parts which differ in width, the presence or absence of a ciliated epithelium and the thickness of the muscular layer; they end in pseudopenises. There is a stalked prostatic gland at the ectal end of each gonoduct, and a diffuse one at the ental end. The diffuse prostate may be absent, in which case the epithelium of the ental part is thickened and glandular. The anterior part of the male gonoduct is found in segment X. The spermatozoa constitute a free mass (Fig, B-C).

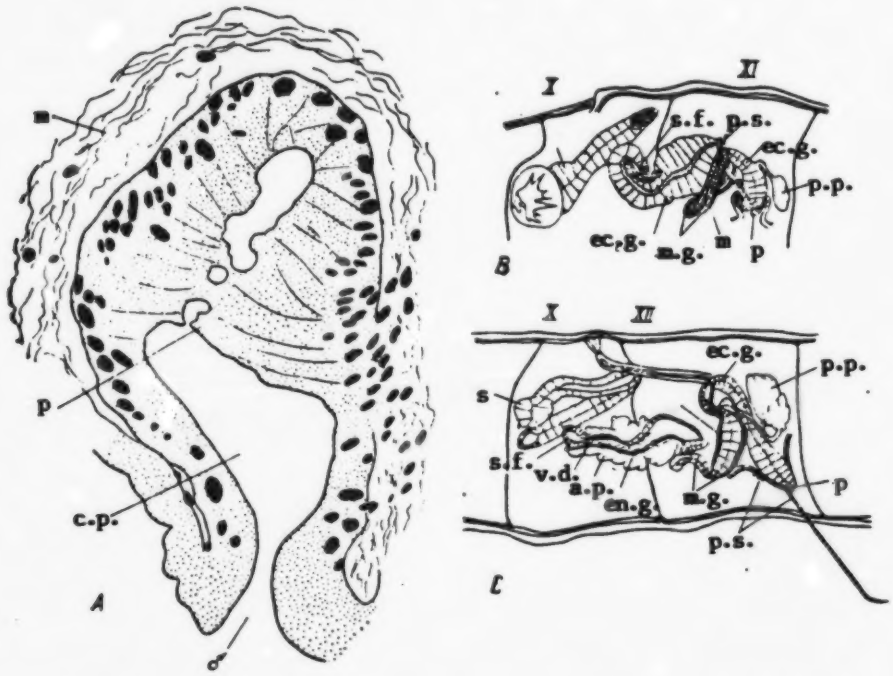
The subfamily is composed of Nootkadrilus Baker and Discordiprostatus Baker.

Baker (1982), who described both genera, assigned them to the subfamily Phallodrilinae on the basis of the presence of a stalked

posterior prostatic gland, the form of the spermathecae, male gonoduct and penial setae, and the absence of large coelomocytes. He believes that Nootkadrilus bears the greatest similarity to Coralliodrilus Erseus, the atrium of which has no prostatic glands, and to Inanidrilus Erseus which has only a posterior prostate, two types of penial setae and muscular spermathecae. In our opinion, the presence of a posterior stalked prostate is the only significant feature (apart from the absence of coelomocytes, which is also characteristic of other subfamilies with the exception of Rhyacodrilinae) common to the Phallodrilinae. A glandular atrial epithelium in the absence of prostatic glands is also known for other tubificids (e.g. Svetlovia and Epirodrilus of the Rhyacodrilinae), as is the muscular efferent part of the spermathecae (Svetlovia). Furthermore, it is difficult to look for some relationship between Nootkadrilus, which probably lost the vas deferens and anterior prostatic gland a second time, and Coralliodrilus, which also lost both prostates of the original form but does have a fairly long vas deferens. It is especially difficult to explain the appearance in the same genus of significant features (glandular epithelium of the gonoduct with no prostate entally and a stalked prostate ectally) of two fairly advanced, and not primitive phallodriline genera such as Coralliodrilus and Inanidrilus. There is no doubt that Nootkadrilus and Discordiprostatus are morphologically similar, the ental parts of their atria are apparently homologous, and so it is even more difficult to pass from the Phallodrilinae to Discordiprostatus, a form with one of the most primitive types of prostates (diffuse) among the Oligochaeta. In any case, it is

(19

very unlikely that such a regression of this important structure to a more primitive state could have occurred within a single subfamily in the absence of other specific phallodriline features.



Structural details of Svetlovia maculata (A), Nootkadrilus hamatus (B) and Discordiprostatus longisetosus (C): A - terminal part of male gonoduct (saggital section); B-C - after Baker, 1982; p.p. - posterior prostatic gland, c.p. - copulatory pouch, m - muscles, m.g. - median parts of male gonoduct, o - male genital aperture, p - pseudopenis, a.p. - anterior prostatic gland, p.s. - penial setae, s - spermatheca, s.f. - sperm funnel, v.d. - vas deferens, ec.g. - ectal part of male gonoduct, en.g. - ental part of male gonoduct

As to the topography of the male gonoduct, we can find no analogy with the mentioned genera amidst the extensive material that has so far been accumulated on the Phallodrilinae. Baker himself writes that the atria of Nootkadrilus are the most complex, and that Discordiprostatus are unique among the Tubificidae. All this has prompted me to introduce a new subfamily for these genera. I would like to note another of their rare morphological characters,

i.e. the partial penetration of the male gonoduct from segment XI into segment X. This characteristic is known in Rhizodrilus and Bothrioneurum in the subfamily Rhyacodrilinae.

TELMATODRILINAE EISEN, 1879

The somatic setae are of different types, i.e. forked, single-toothed, scopiform, hairlike. Genital setae are often present. The prostatic glands are compact, stalked, and may number up to 16 on each atrium. The atria end in a penis or pseudopenis. Spermatozoa or vermiform spermatozeugmata are present. This subfamily consists of the genera Alexandrovia Hr. and Telmatodrilus Eisen. Holmquist (1974) proposes that Telmatodrilus be broken down into two genera.

LIMNODRILOIDINAE ERSEUS, 1982

The somatic setae are exclusively forked, occasionally with a ligament between the lower tooth and the shaft of the seta. Genital setae are rarely encountered. The oesophagus in segment IX is modified, either inflated and glandular, or with a pair of lateroventral diverticula directed anteriorly toward dissepiment 8/9. The prostatic gland is attached to the atrial ampulla, usually by its wide base, but in some cases with the help of a fairly narrow sphincter, and is connected with the modified internal epithelium of the ampulla, which forms a characteristic lining with a granular structure (prostatic pad), or with the atrial diverticulum which also has a granular lining. The atria end mostly in a pseudopenis or pores, very rarely in a true penis. The spermatozoa constitute a free mass, clusters, or in rare cases simple spermatozeugmata.

The subfamily includes Limnodriloides Pierant., Marcusaedrilus Righi et Kanner, Tectidrilus Erseus, Thalassodrilides Brink. et Baker, Smithsonidrilus Brinkhurst, Kaketio Righi et Kanner, Parakaketio Erseus and Doliodrilus Erseus.

AULODRILINAE HRABE, 1967

The somatic setae are forked, oar-shaped, fan-shaped, hairlike. Genital setae are rare. There are 1-3 pairs of testes and one pair of ovaries. The prostatic gland has a narrow or wide stalk. The atria end in penises which often have a chitinous cover. One, rarely two pairs of spermathecae are present. The species of Aulodrilus reproduce mainly architomously, less commonly sexually. Their genital organs are usually displaced anteriorly by several segments. At the posterior end of the body we sometimes find an unsegmented zone which functions as gills.

This subfamily includes the genera Aulodrilus Bretscher, Peipsidrilus Timm, Neoaulodrilus Giani, Martinez-Ansemil, Moubayed et Dia and Sketodrilus Karaman. The last two genera are very similar, so perhaps they should be combined in a single genus.

TUBIFICINAE EISEN, 1879

These are the higher tubificids. The somatic setae are forked, single-toothed, fan-shaped, hairlike. Genital setae are usually scarce, or often absent. The compact stalked prostatic gland opens into the atrium medially or in the ental half, and is sometimes absent. The atria end in penises enclosed in penial bursae. The penises may have a chitinous cover or tube. Architomous reproduction is encountered.

The subfamily includes the genera Tubifex Lamarck, Limnodrilus Clap., Isochaetides Hr., Potamothrix Vejd. et Mrazek, Psammoryctides

Vejd., Ilyodrilus Eisen, Clitellio Sav., Clitelloides Finogenova, Tubificoides Last., Spirosperma Eisen, Peloscolex Leidy, Baikalodrilus Holmquist, Haber Holmquist, Antipodrilus Brinkhurst, Lycodrilus Grube, Lycodrilides Hr., Tubipenifer Semernoi, Arctodrilus Brinkh., Spirospermoides Dumnicka, Krenedrilus Dumnicka and Varichaetadrilus Brinkh. (=Ilyodriloides Sok.).

Thus, the Tubificidae family is known to consist of seven subfamilies which together include 72 genera. Phallodrilinae, Limnodriloidinae and Nootkadrilinae include only marine or brackish-water genera (with individual species that inhabit fresh waters as well); Aulodrilinae and Telmatodrilinae include only freshwater species, while Rhyacodrilinae and Tubificinae contain both freshwater and marine forms, as well as several genera with mixed ranges. At the present time, we know of 35 marine and 33 freshwater genera of tubificids, as well as 4 genera common to both sea and fresh waters.

It is still difficult to speak of the phylogenetic relations of the subfamilies, but there is no doubt that the habit of the Rhyacodrilinae is the most primitive. Despite the known features of specialization, here we come up against the greatest number of primitive features of organization, including the absence of a separate prostatic gland, the presence of spermatozoa, weak differentiation of the penial appartus, metamerism of the gonads (e.g. Svetlovia, Bothrioneurum), the ectal entry of the vas deferens into the atrium, probably the location of the spermathecal apertures in the anterior part of segment X, the presence of large coelomocytes and the formation of morulae of oocytes. Another distinctive feature of the Rhyacodrilinae is morphological

flexibility which is seen particularly in the extreme diversity of the forms and structures of the generative apparatus.

The closest to the Rhyacodrilinae are the Phallodrilinae and Nootkadrilinae which, despite the development of certain progressive characters such as compact prostates and a complex penis (Aktedrilus), have retained quite a number of primitive features; both subfamilies have spermathecal pores at dissepiment 9/10, both have spermatozoa, Nootkadrilinae have an anterior diffuse prostate, and Phallodrilinae have an ectal entry of the vas deferens into the atrium, both a penis and simple pores and aberrant metamerism of the gonads. The Limnodriloidinae, Aulodrilinae and Telmatodrilinae are farther away from the Rhyacodrilinae, though they also have much in common with them. Though it is narrower and compact, the prostatic gland in Limnodriloidinae is attached quite extensively to the atrium; in Telmatodrilinae, the spermathecal apertures are located at the anterior dissepiment and the atrium is pyriform; gonadal metamerism is observed in the Aulodrilinae; all of these subfamilies have spermatozoa (in addition to spermatozoa, vermiform spermatozeugmata are also found in the genus Alexandrovia of the subfamily Telmatodrilinae). Finally, in the most advanced subfamily Tubificinae, ancestral features can be found with difficulty, sooner in the form of an atavism. For example, as an exception, the spermathecal apertures in individual species of the Tubificinae are located near dissepiments 9/10 or 10/11, instead of medially.

(201

Analogous structures developed in a similar manner in different lines of both marine, and freshwater tubificids. This applies to the differentiation of the terminal part of the male

gonoduct from simple pores to a complex penis (Phallodrilinae, Rhyacodrilinae, Limnodriloidinae), the secondary reduction of the prostatic gland (Rhyacodrilinae, Phallodrilinae, Tubificinae), the concentration of spermatozoa from a disorganized mass into organized clusters and then into spermatozeugmata (Rhyacodrilinae, Telmatodrilinae, Phallodrilinae, Limnodriloidinae), the development of an unpaired spermatheca or the complete disappearance of spermathecae (Rhyacodrilinae, Phallodrilinae, Limnodriloidinae), the formation by the integuments of a special secretion to which particles of the substrate adhere (Telmatodrilinae, Phallodrilinae, Limnodriloidinae, Tubificinae), the fusion of the genital apertures into one (Rhyacodrilinae, Phallodrilinae, Limnodriloidinae), and to a number of other characteristics. The nature of these changes (the result of convergent or parallel development) is still not always clear, despite the fact that our ideas of the structural potentials of the Tubificidae have greatly expanded over the past few years. For example, we learned just recently of the development of spermathecae behind the male genital apertures in segment XII in tubificids. A particularly large number of facts related to new morphological characters previously unknown in tubificids can be found in the descriptions of marine genera, which I have noted in the diagnoses of the marine subfamilies (setae with a ligament, diverticula on the intestine and atrium, the absence of an intestine, etc.). Further detailed research of the freshwater and marine fauna will definitely clarify many of the questions pertaining to the systematics and phylogeny of this group of animals.

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ON DIAGNOSTIC CHARACTERS OF SUBFAMILIES IN THE FAMILY TUBIFICIDAE (OLIGOCHAETA)

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Summary

The most important characters which have been used in the key of subfamilies in the family Tubificidae are the following: presence or absence of large coelomocytes in the body cavity; method of attachment; shape and number of the prostatic glands on each male gonoduct; localization of the seminal receptacle pores; type of the male genital cells. A new subfamily, the Nootkadrilinae subfam. n., has been created for two marine genera, *Nootkadrilus* Baker and *Discordiprostatus* Baker. A list of genera in all seven subfamilies is presented. The description of *Svetlovia maculata* Cekanovskaja is corrected and supplemented with new details on the basis of reinvestigation of the holotype of this species.